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A note on aquatic and aerial vision in Odontocetes

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The paper by NEUHAUS, which recently (1986) appeared in this journal, contains an over simplified analysis which casts doubt on some of its conclusions. The author presents calculations, based on the anatomy of the eye of the Beluga (White Whale, *Delphinapterus leucas*), from which it appears that the eye is approximately in focus (i.e. well focused on objects at infinity), when it is used under water. Lacking a mechanism for accommodation, it follows that in air, where refraction by the cornea becomes effective, the Beluga must be very near-sighted. This conclusion, however, conflicts with the Beluga's apparent use of vision in air. The author proposes a resolution to this conflict by first assuming that the image formed by the eye under water lies on a flat surface slightly forward of the retina and perpendicular to the optical axis. This paraxial image plane intersects the retina slightly to the side of the optical axis and thus avoids the "blind spot" resulting from the axial location of the optic nerve. Carrying this idea further, the author then reasons that the Beluga could be in focus in air also. That is, as the paraxial image plane moves much closer to the lens, with the addition of the refractive power of the cornea in air, it will again intersect the retina at some greater annular distance from the optical axis. The reader is led to believe that irrespective of the viewing medium or distance the non-focusing eye of the Beluga will be in focus somewhere on the retina (with the underlying assumption that these regions of the retina are capable of good resolution). These ideas were not supported by new data and are inconsistent with a more general geometrical optics analysis. Fundamentally, the assumption that the image is focused on a flat surface is in error and the inferences based on this assumption are also incorrect. Images formed by simple optical systems are projected on a curved surface (which might well be the very reason for the curved shape of the vertebrate retina). This phenomenon is known as the Petzval curvature of the image. For a plane object at infinity and a system of k refracting surfaces, the radius of curvature of the final image in the absence of oblique astigmatism and spherical aberration can be calculated with the following equation (LONGHURST 1967, p. 359–360):

$$\frac{1}{R_k} = n_k \sum_{i=1}^{k-1} \frac{1}{r_i} \left(\frac{1}{n_{i+1}} - \frac{1}{n_i} \right),$$

in which R_k is the radius of curvature of the image in the k^{th} medium, r_i is the radius of curvature of the i^{th} refracting surface and n_i is the refraction index after the i^{th} refracting surface. Applying this equation to the eye of the Beluga as described by NEUHAUS, for aquatic vision a Petzval curvature of the retinal image is 10.0 mm. In view of the uncertainty of the values used in the calculation, the result may be considered to be in reasonable agreement with the curvature of the retina, which has, according to NEUHAUS, a radius of 11.3 mm. We may conclude that the Beluga eye under water is in focus over the entire retinal surface (as could be expected a priori). This near coincidence of the retina and under water image eliminates the need to seek a mechanism to avoid the axially located

"blind spot" caused by the optic nerve. The other key feature of the NEUHAUS Beluga eye model is that it would be focused in air. However, the aerial Petzval image curvature of the NEUHAUS eye model indicates that the animal is hopelessly near-sighted in air.

One would expect toothed whales to have good far vision in air because echo location does not provide remote sensory information in this medium and good near vision in water because the oceans attenuate light rapidly with distance. In this regard the eye model presented by RIVAMONTE (1976) offers an alternative explanation which agrees with the behaviorally measured near-sightedness in water and far-sightedness in air results of HERMAN et al. (1975). In this model of the eye of the bottle-nosed dolphin (*Tursiops truncatus*), the lens is assumed to be bi-focal, the core having an appreciably higher refractive index than the periphery. The lens core would be primarily functional in aquatic vision, allowing focused near vision under water. By virtue of the peculiar shape of the pupil and location of the lens, in air the image forming light would mainly pass through the less refractive peripheral part of the lens. The combination of a less refractive lens periphery and highly refractive cornea allows focused far vision in air. As argued elsewhere (DRAL 1985), the elements of this model fit nicely into the known facts of ocular anatomy, enhancing its credibility.

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